Effects of an Inert, Palatable Resource Subsidy on Live Prey Selection by Juvenile Fish

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Abstract

Resource subsidies, defined as energy and nutrients that enter ecosystems from external sources, can have diverse and complex effects on consumer populations. For example, resource subsidies can increase consumer growth rates and survival by direct ingestion of the subsidy or by increasing populations of other natural prey. Excessive rates of resource subsidy addition, however, can reduce habitat quality through eutrophication. In this study, I tested the effects of three different rates of manufactured feed (i.e., a resource subsidy) provision (no feeding, 1%, or 3% body-weight/day; BW/d) on the foraging habits and growth rates of age-0 channel catfish (*Ictalurus punctatus*) in earthen ponds. I hypothesized that increased feeding rates would increase populations of zooplankton prey in ponds; alter the amount, composition, and preference of natural prey ingested by the fish; and reduce dissolved oxygen concentrations in ponds. I found that increasing the feeding rate did not increase the density or alter community composition of zooplankton in ponds. Although the feed was ingested by fish in the 1% and 3% BW/d ponds and increased fish growth, fish in all feeding treatments still ingested the same types and amounts of natural prey as they grew through time. Surprisingly, the fish ingested larger insects and chironomid larvae during early life and then switched to smaller zooplankton later, opposite of the pattern that has been observed for most other fishes. Finally, increasing the feeding rate decreased dissolved oxygen concentrations in ponds. From an applied aquaculture perspective, natural prey may have an important role in the growth of juvenile channel catfish. Future studies should further examine the interactive effects of resource subsidies, habitat quality, and consumer ontogeny on diet patterns in highly subsidized ecosystems.

Introduction

The structure and function and aquatic and terrestrial ecosystems are often tightly interconnected by energy and nutrient flux between them (Nakano and Murakami 2001). Aquatic ecosystems can be highly subsidized by terrestrial resources (e.g., leaf litter, woody debris, and detritus) produced in their watersheds because of their downhill position in the landscape (Vanni et al. 2005). In turn, organisms (e.g., insects, fish) produced in aquatic ecosystems can enhance terrestrial productivity, especially in nutrient-limited riparian zones (Christie et al. 2008). In both ecosystems, the availability of biologically-fixed energy and nutrients are primary determinants of consumer growth rates, densities, and biomass. Thus, the timing and magnitude of resource delivery across ecosystem boundaries can drive the structure of populations and community interactions (Nowlin et al. 2008).

The consequences of resource subsidies for aquatic ecosystems can be diverse and complex. For example, consumers can directly benefit from palatable resources by incorporating them into the diet (Vanni et al. 2005; Richardson et al. 2010). Indirectly, resource subsidies can also reduce a consumer's energetic foraging costs by augmenting local prey densities through bottom-up effects (Nakano and Murakami 2001; Richardson et al. 2010). In low-order streams, for example, allochthonous material such as insects and leaf litter can serve as food for fish, or enhance *in situ* production of other prey (England and Rosemond 2004). In another example, Graham et al. (2006) showed that conifer pollen inputs to small boreal lakes subsidized littoral nutrient levels and increased algal growth and zooplankton abundance.

Resource subsidies that have high contents of nitrogen (N) and phosphorus (P), which classically limit primary productivity in aquatic ecosystems (Vollenweider 1968; Schindler 1977), can initiate bottom-up effects in food webs by increasing abundance of autotrophs and/or

heterotrophs that are food for zooplankton (Qin et al. 1995). In turn, enhanced zooplankton abundance can increase fish early life growth and survival, and ultimately drive the year-class strength of populations (Beaugrand et al. 2003; Kallasvuo et al. 2010). Thus, resource subsidies can drive ecosystem dynamics through direct responses. Alternatively, resource subsidies can affect aquatic ecosystems through more complex, indirect interactions. For example, fish that switch their diets to leverage an ephemeral resource subsidy can release their former invertebrate prey from predation pressure, thereby causing increases in the prey populations (Rejas et al. 2005).

Size-selective predation by fish can be particularly important for structuring the size distribution of their zooplankton prey populations. Brooks and Dodson (1965) found that small-bodied zooplankton genera, such as *Bosmina*, dominated lakes colonized by alewife along the east coast of the USA. In non-alewife lakes, however, larger *Diaptomus* and *Daphnia* were most abundant. Brooks and Dodson inferred that their observation was caused by size-selective predation by alewives, such that large-bodied zooplankton genera (e.g., *Daphnia*) were favored as prey in mixed communities. In the absence of size-selective predation by fish, however, the ability of large zooplankters to graze more efficiently and utilize larger sizes of particulate organic matter allows them to out-compete smaller taxa like *Bosmina*. The criteria of prey selection can also include their visibility (O'Brien et al. 1976). For example, female zooplankters can have different vulnerabilities to visual predators based on the presence or absence of the large and often pigmented egg masses (Hairston et al. 1983; Vuorinen et al. 1983; Bollens and Frost 1991).

In addition to having complex effects on food web interactions, resource subsidies can negatively impact ecosystem function through eutrophication, whereby excessive nutrient

loading increases primary productivity to undesirable levels, destabilizing food webs and decreasing water quality (Vollenweider 1968; Cole and Boyd 1986; Ludsin et al. 2001). For example, excessive nutrient pollution from watershed runoff causes seasonal hypoxia (dissolved oxygen, DO < 2 mg/L) in the central basin of Lake Erie, the Gulf of Mexico, Chesapeake Bay, and the Neuse River Estuary (Ludsin et al. 2009). In turn, hypoxia can strongly impact fishes through direct effects on physiology, growth and survival, or by modifying their foraging behavior and spatial overlap with optimal temperatures and/or suitable prey (Kramer 1987; Burleson et al. 2001; Thomas et al. 2007; Brandt et al. 2009).

In this study, I tested the effects of a palatable resource subsidy on the interaction between fish predators and their zooplankton prey. I chose to model this interaction using manufactured feed (i.e., a resource subsidy) addition to earthen ponds stocked with age-0 channel catfish (*Ictalurus punctatus*). I had three main hypotheses for this study that I tested through providing three different feeding rates to ponds (no feeding, 1%, or 3% body-weight/day; BW/d). First, I hypothesized that adding the manufactured feed to ponds would change zooplankton community composition and increase zooplankton densities by fertilizing the ponds. Second, I hypothesized that the feed would alter the amount, composition, and preference of live prey ingested by fish through time. Third, I hypothesized that increased manufactured feeding would decrease DO and increase free ammonia (a toxic nitrogenous waste; Smart 1978) concentrations in ponds, reducing the amounts of feed and live prey ingested by fish.

Materials and Methods

Study site and experimental design

The feeding experiment was conducted during July–September 2010 at the Hebron State Fish Hatchery (SFH), central Ohio, managed by the Ohio Department of Natural Resources-Division of Wildlife (DNR-DOW). Water for filling ponds was supplied by a nearby eutrophic reservoir, Buckeye Lake, via a 1.5-mile extant section of the Ohio Erie Canal. The earthen ponds at Hebron SFH are rectangular, 0.4 ha, have a maximum depth of 1.5 m near the concrete kettles (a rectangular draining basin), and contain 2,945 m^3 of water. The fill water passed through a 0.5-mm mesh screen to prevent large organisms from entering the pond.

Nine ponds were filled 7 d prior to stocking 14 day-old channel catfish at 13 fish/m^3. Fish were produced by captive brood stock at the Senecaville SFH (DNR-DOW) in eastern Ohio. Three ponds were randomly assigned to feeding treatments of no feeding whatsoever, 1%, or 3% body-weight/day (BW/d), with the feed provided 5 days per week. The commercial sinking feeds were hand broadcast to the ponds from the concrete kettles between 1200 and 1400 hours. Diet formulations, granular sizes, and feeding rates were adjusted biweekly to match fish growth (Appendix A). To avoid fish kills, all ponds received simultaneous short-term (< 6 hour) paddlewheel aeration when DO concentrations fell below 1 mg/L. Aeration was typically initiated between 0600 and 0800 hours, lasted for 2–4 h until DO was > 4 mg/L, and was infrequent (2–3 times/week, primarily during the late culture weeks).

Effects of feeding rate on zooplankton abundance and community composition

Zooplankton was sampled in each pond weekly using a 0.5-m diameter 64-μm mesh net fitted with a mechanical flow meter (Model 2030R, General Oceanics, Inc., Miami, Florida). The net was repeatedly raised and lowered as it was dragged across each pond to achieve depth-integrated collections. Samples were preserved in the field using sugar formalin (Haney and

Hall 1973) and enumerated in the laboratory following the procedure described by Tew et al. (2010). The dry weight of each taxon was determined using length-dry weight regressions (Culver et al. 1985). Secondary productivity of crustacean zooplankton was calculated as a function of biomass and water temperature (Jacob and Culver 2010).

To quantify the effects of feeding rate on zooplankton in ponds, I compared the density and biomass of major zooplankton groups (e.g., cyclopoids, rotifers, etc.) among treatments using the following linear mixed effects model (MEM):

$$Y_{ijk} = \beta_0 + T_i + \beta_1 D_j + \beta_2 (TD)_{ij} + Z_k + \varepsilon_{ijkl}$$

where Y is the response variable (i.e., density or biomass), β_0 is the grand mean, T (Treatment) is the fixed effect of the feeding-rate treatment, D (Date) is the fixed effect of time, TD is the fixed effect of the treatment × time interaction, Z is the random effect of pond, and ε is the unexplained error. To determine the effects of feeding rate on community composition in ponds, I used non-metric multidimensional scaling (NMS) to ordinate the weekly samples from each pond in zooplankton-species space. I then used the MEM to test for differences in NMS axis scores among treatments and through time (Rettig et al. 2006). I tested all data used in the MEM for normality using one-sample Kolmogorov-Smirnov tests, and I assessed equality of variance by visually examining residual plots. To perform the NMS, I first $\log_{10}$-transformed all the raw data, then I used the "slow and thorough" setting with the Sorensen Bray-Curtis distance measure. I performed the MEM tests in IBM SPSS Statistics Version 19 (IBM, Armonk, New York) and NMS in PC-ORD Version 5 (MjM Software Design, Gleneden Beach, Oregon).

Effects of feeding rate on fish growth, diets, and prey preference

Ten fish were collected from each pond weekly using dip nets (0.5-m length × 1-m width, 0.2-cm mesh) between 1400 and 1800 hours, within 3 hours after a feeding event. In the laboratory, each fish was measured (total length) and weighed, then preserved in formalin for later gut content analysis. To account for the effects of fish size on diet selection, the largest, medium, and smallest fish by wet weight were selected for gut content analysis from each weekly pond collection. The entire alimentary canal was removed from each fish, the gut contents were removed, and the empty gut was weighed for each fish. The difference between the pre-gut removal weight and post-gut removal weight + the empty gut weight was used to estimate the total wet weight of the gut contents for each fish.

The gut contents were suspended in water and spread evenly in a plankton counting wheel for examination under a stereomicroscope at 50X magnification. Prey were identified to the lowest taxonomic level possible (usually genus or species), counted, and up to 20 individuals of each taxon were measured. I used taxon-specific length-dry weight regressions to calculate the biomass of zooplankton (Culver et al. 1985) and other invertebrate prey (Appendix B) ingested by fish. I assumed that the weight of feed in each fish's gut contents was equivalent to the difference between the weight of the entire gut contents and the weight of the identified natural prey estimated from length-weight regressions, adjusted for the weight of unidentified natural prey ingested by fish in the no-feeding treatment.

I sorted prey types identified in the fish guts into major taxonomic groups (e.g., cladocerans, copepods, insects, ostracods, other natural prey, and manufactured feed) and calculated the percentage of each group to the total diet by biomass for each feeding treatment. I also used NMS to ordinate the diets of fish in prey species space to test for differences among the suite of prey ingested by fish across treatments and through time. To determine whether

differences in fish diets across ponds were related to differences in the ponds' zooplankton communities, I performed a Mantel test to correlate the distance matrices derived from the fish diet and pond zooplankton datasets. I performed the Mantel test in PC-ORD 5 using the Sorensen Bray-Curtis distance measure.

To determine the fish's taxonomic preference for zooplankton prey, I calculated Chesson's α_i (1983),

$$\alpha_i = (r_i / n_i) \; / \; \sum_{j=1}^{m} (r_j / n_j), \quad i = 1, \ldots, m$$

where r_i and n_i are the number or proportion of prey type i in the fish's gut and in the pond environment, respectively. To more clearly display prey preference, I then used a_i values to calculate the electivity value, ε_i, for each prey type (Chesson 1983),

$$\varepsilon_i = (m\alpha_i - 1) / ([m - 2]\alpha_i + 1), \quad i = 1, \ldots, m$$

where if $a_i = 0$, then $\varepsilon_i = -1$ (negative selection when $\varepsilon_i < 0$); if $a_i = 1/m$, then $\varepsilon_i = 0$ (neutral selection); and if $a_i = 1$, $\varepsilon_i = 1$ (positive selection when $\varepsilon_i > 0$).

To determine the size-based preferences of fish for zooplankton prey, I divided the zooplankton in diets and ponds into six equal 0.2-mm size bins and calculated electivity values (ε) for each size bin. I also pooled all the zooplankton size measurements from the fish diets and the pond net collections to compare the size distributions of the most abundant taxa in the diets to those in the ponds using two-sample Kolmogorov-Smirnov tests.

Effects of feeding rate on dissolved oxygen and free ammonia concentrations

Dissolved oxygen was measured in each pond three times weekly (Monday, Wednesday, Friday) from the kettle using a membrane electrode attached to a YSI model 556 hand-held meter

(Yellows Springs, Ohio) at the surface and at 1 m depth during morning (0700–0900 hours). Total ammonia nitrogen (TAN) was measured weekly in each pond from unfiltered water samples collected during afternoon using the fluorometric method, Protocol B, described by Holmes et al. (1999). Water temperature was measured continuously using data loggers (HOBO loggers, Onset, Pocasset, Massachusetts) suspended at 0.5-m depth in each pond, while afternoon pH was measured using a membrane electrode. Free ammonia concentrations were calculated from TAN measurements using temperature and pH-dependent equilibria (Emerson et al. 1975). I used the MEM to test for differences in dissolved oxygen and free ammonia among feeding treatments and through time.

Results

Effects of feeding rate on zooplankton abundance and community composition

Total cladoceran and copepod densities did not differ across feeding treatments (MEM, treatment × time, both $P > 0.6$; Fig. 1), although zooplankton community composition changed substantially through time in all ponds. *Moina* were initially abundant, but then decreased and were essentially absent by week 5 (MEM, time, $P < 0.001$; Fig. 1). After *Moina* populations declined, *Bosmina* and chydorids increased (MEM, time, both $P < 0.001$) and were the predominant cladocerans in ponds during weeks 5–7. Total cladoceran density increased during week 5–7 and copepod density spiked during week 3 in the no-feeding ponds (Fig. 1). Secondary productivity of crustaceans did not differ across feeding treatments through time (MEM, treatment × time, $P = 0.8$).

I performed NMS to reduce the original zooplankton abundance dataset into fewer dimensions (i.e., axes) that I then used to test for differences in community composition among

feeding treatments and through time. The final solution of the NMS had reasonably low stress (13.7) with two dimensions that explained 92% of the variation in distance of the original dataset. Axes 1 and 2 did not differ across treatments through time (MEM, treatment × time, both $P > 0.5$; Fig. 2). However, both axes were correlated with *Moina* abundance in ponds, showing a general transition from *Moina* to other cladocerans and copepods through time (Fig. 2).

Effects of feeding rate on fish growth, diets, and prey preference

Fish growth in total length and wet weight was greater in the 3% and 1% BW/d treatments as compared to fish in the no-feeding treatment (MEM, treatment × time, both $P < 0.001$; Fig. 3), However, the dry weight of identifiable natural prey in the gut contents did not differ across feeding treatments (MEM, treatment × time, $P = 0.9$; Fig. 4a), and did not change through time (MEM, time, $P = 0.3$). Expressed as % fish body weight (BW), natural prey ingested decreased through time (MEM, time, $P < 0.001$) and also did not differ across feeding treatments (MEM, treatment × time, $P = 0.9$; Fig. 4b).

Although manufactured feed ingested by fish increased through time (expressed as dry weight and % BW; MEM, time, both $P < 0.001$), it did not differ between fish in the 1% and 3% BW/d ponds (MEM, treatment × time, both $P > 0.3$; Fig. 4c,d). The total amount of food ingested by fish increased through time (MEM, time, $P < 0.001$), and was higher for fish in 3% and 1% BW/d treatments as compared to fish in the no-feeding treatment (MEM, treatment × time, $P < 0.012$; Fig. 4e). Expressed as % BW, the total amount of food ingested decreased then increased through time (MEM, time^2, $P < 0.001$; Fig. 4f). Amounts of natural prey, manufactured feed, or total food ingested were not correlated with DO concentrations in ponds (all $P > 0.2$).

The predominant natural prey items ingested by fish in all treatments during the experiment were insects, mainly chironomid larvae (Fig. 5). To further test for differences in the suite of natural prey ingested by fish across feeding treatments through time, I used NMS to derive fewer dimensions of prey assemblages in the fish diets. The final NMS solution for fish diets had reasonably low stress (13.0) with three dimensions (axes) that cumulatively explained 88% of the variation in distance of the original dataset. There were no differences across feeding treatments through time for any of the axis scores (MEM, treatment × time, $P = 0.6$; Fig. 6), meaning natural prey composition in the fish diets did not differ across feeding treatments. Scores for Axis 2, which explained most of the variation in the original dataset, decreased through time (MEM, time, $P < 0.001$), showing a strong dietary transition from chironomid larvae to small cladoceran zooplankton as the experiment progressed. Axis 1 and 3 scores, which explained lesser variation in diet composition, did not change through time (MEM, time, $P > 0.9$; Fig. 7), suggesting factors other than time were underlying the differences in fish diet composition explained by these axes.

To identify factors potentially driving differences in diet composition across ponds and dates, I correlated the fish diet NMS axis scores of fish diets with temperature, DO concentrations in ponds, and fish weight. Axis 2 was negatively correlated with fish weight (Fig. 7a), which provides complementary evidence that as fish grew in size they increasingly incorporated small crustacean zooplankton (e.g., *Bosmina*, chydorids) in their diets. Axis 3 was negatively correlated with DO concentration (Fig. 7b), showing that fish ingested the most benthic cladocerans, insects, and copepods when DO concentrations were highest in ponds. Temperature was not significantly correlated with any NMS axis. Further, the fish diet and pond zooplankton distance matrices were positively correlated (Mantel test, $r = 0.27$, $P = 0.001$),

showing that ponds with more dissimilar zooplankton communities contained fish with more dissimilar diets.

As a function of feeding rate treatment, there were no apparent differences in fish electivity values for zooplankton taxa (Fig. 8). The fish had neutral or positive selection for chydorids throughout the experiment and *Acanthocyclops vernalis* during weeks 1 and 2. However, the fish had negative selection for *A. vernalis* during weeks 3–7, and also selected against *Bosmina*, *Mesocyclops edax*, and *Skistodiaptomus pallidus* throughout the experiment (Fig. 8). Although *Moina* were abundant in ponds during the early weeks in ponds, they were not included in diet electivity calculations and the diet NMS because they contributed < 0.5% of the total biomass of natural prey in the fish gut contents.

I also found no differences in the size preferences for zooplankton prey by fish across feeding rate treatments (Fig. 9). During weeks 3–6, fish had positive selection for 0.1–0.3 mm zooplankton that included mainly chydorids. However, the fish showed negative or neutral selection for zooplankton > 0.3 mm throughout the experiment. With the exception of *S. pallidus*, zooplankton in the fish diets were consistently larger than those collected in ponds using nets (two-sample Kolmogorov-Smirnov tests, all $P < 0.001$; Fig. 10), which suggests the fish generally selected for the largest individuals of a given taxon within the ponds.

Effects of feeding rate on dissolved oxygen and free ammonia concentrations

Dissolved oxygen concentrations in the 1% and 3% BW/d ponds (Fig.11) were lower through time as compared to the no-feeding treatment (MEM, treatment × time, $P < 0.001$; Fig. 11b). During weeks 6–8, DO concentrations ranged 4–6, 2–5, and 0–2 mg/L in the no-feeding, 1%, and 3% BW/d ponds, respectively. Free ammonia concentrations were < 15 µg N/L in all ponds

during weeks 1–6 and were not different across treatments (MEM, treatment × time, $P = 0.3$), but spiked in all ponds during weeks 7 and 8 (Fig. 11c). Mean surface temperatures ranged 24–31°C during the experiment, and decreased through time (Fig. 11a).

Discussion

Effects of feeding rate on zooplankton abundance and community composition

Flux of resource subsidies, such as terrestrial leaf litter to streams and adult aquatic insects to riparian predators, are examples of important links between adjacent ecosystems (Richardson et al. 2010). In general, spatial movements of nutrients, detritus, and prey organisms across the interface of contiguous habitats can influence the dynamics of consumer populations (Polis and Hurd 1996; Polis et al. 1997). In particular, consumers in relatively low productivity habitats are often subsidized by the transport of food resource from other, more productive habitats (Polis et al. 1997). For example, migratory sockeye salmon *Oncorhynchus nerka*, deliver marine-derived nutrients to the streams in which they spawn and die, and these resource subsidies can increase the abundance of stream biota (Tiegs et al. 2009). In Alaskan lakes, Chen et al. (2011) demonstrated that zooplankton production was significantly higher after the introduction of sockeye salmon (*Oncorhynchus nerka*). Chen et al. also found that increased density of spawning salmon elevated the influx of nitrogen and, in turn, zooplankton production over the past few centuries. Hann et al. (1994) studied the community response of cladoceran zooplankton to high nitrogen and phosphorus inputs in experimental lakes in Ontario, and found that nutrient flux and other factors (e.g., light penetration, pH) were important determinants of cladoceran community structure.

In this study, I considered manufactured feed as a resource subsidy that adds nutrients to the pond environment. I hypothesized that the feed would change community composition and increase zooplankton abundance by fertilizing ponds. However, I found that adding the feed to ponds at two different rates did not increase zooplankton density or change community composition relative to the no-feeding ponds. This may indicate that (1) the ponds were not initially nitrogen or phosphorus limited, (2) nutrients in the feed did not increase or change populations of phytoplankton and bacteria that serve as food for zooplankton, (3) other factors like temperature and light play an paramount role in influencing zooplankton abundance and community composition (Hann et al. 1994), and/or (4) top-down predation pressure from channel catfish overwhelmed the bottom-up effects of increased feeding rate. Further studies should address these possible reasons why feeding rate does not affect zooplankton in ponds.

Effects of feeding rate on fish growth, diets, and prey preference

There are large qualitative differences in the types of resource subsidies, and they vary in the magnitude and types of effects they elicit in recipient ecosystems (Richardson et al. 2010). For example, terrestrial invertebrates are known to be important prey for stream fishes (Cloe and Garmen 1996; Wipfli 1997; Nakano et al. 1999; Kawaguchi and Nakano 2001). Kawaguchi and Nakano (2001)'s study conducted in streams showed that terrestrial invertebrates were a major contribution to rainbow trout (two *Oncorhynchus* spp.) and charr (two *Salvelinus* spp.) diets in summer, and rainbow trout and charr ingested almost 50% of the annual total input of terrestrial invertebrates from riparian forests and grasslands into streams, making this subsidy critical for the stream salmonid populations. However, some subsidies are not equally utilized by all consumers. In Iliamna Lake, Alaska, Denton et al. (2010) showed that charr (three *Salvelinus*

spp.) utilized larger sockeye salmon (*Oncorhynchus nerka*) eggs and carcasses to varying degrees based on their feeding ecology.

In addition to qualitative differences in resource subsidies, they can also have different effects on consumers based on the consumer's feeding ecology and seasonal delivery patterns. Romero et al. (2005) showed that coastal cutthroat trout (*Oncorhynchus clarki clarki*) in streams with vegetation cover ingested twice the amount of aquatic invertebrates in winter and spring as compared to during summer and fall. In their study, trout diets changed seasonally between terrestrial invertebrates (a resource subsidy) and aquatic invertebrates (natural prey), based on their relative availability. In a different study, Pihl (1994) showed that dietary composition of several fish species (Atlantic cod *Gadus morhua*, whiting *Merlangius merlangus*, and American plaice *Hippoglsssoides platessoides*) was determined by prey community structure and availability, and that low oxygen changed diet composition.

I hypothesized that the manufactured feed added to ponds would alter the amount, composition, and preference of live prey ingested by fish through time. However, I found that catfish ingested a fixed amount of natural prey, regardless of the amount of supplemental feed added to ponds, even though the amount of feed ingested increased through time. This indicates that natural prey are important to catfish diets, even in intensive pond culture. Further, I found that the preference of catfish for live prey by both taxon and size did not change with the amount of feed added to ponds.

Given that natural prey were actively ingested by fish in all ponds, what factors influenced their diet composition through time? I found evidence that environmental zooplankton abundance and composition, DO concentration, and ontogeny of the fish all influenced the diet. For example, catfish favored benthic prey when DO concentrations were

high. Contrary to other fishes that are zooplanktivorous during early life (Mayer and Wahl 1997; Pilati and Vanni 2007), I found that the catfish first ingested insects in ponds, and then switched to zooplankton. Because fairly large insect larvae were first ingested by fish, gape size apparently did not limit ingestion of live prey in the ponds. However, I first collected fish when they were about 3 weeks old, so they may have been gape limited earlier in life and previously undergone the expected switch from zooplankton to insects.

Effects of feeding rate on dissolved oxygen and free ammonia concentrations

Dissolved oxygen (Kramer 1987; Andrews and Matsuda 1975) and free ammonia (Hargreaves and Kucuk 2001) concentrations can strongly affect the activity, growth, and survival of fish. I hypothesized that increased feeding would decrease DO concentrations and increase free ammonia concentrations in ponds, reducing the fish's ingestion of the feed and live prey. Although ponds that received manufactured feeds had low DO concentrations, free ammonia concentrations were similar across feeding treatments. Free ammonia concentrations spiked in all ponds at the end of this study, which may have been caused by organic matter decomposition (Gudimov et al. 2010). It is yet unclear whether DO and free ammonia concentrations affected fish growth and survival in the ponds.

Conclusions

I studied the diet patterns of age-0 channel catfish in ponds that received different amounts of a palatable resource subsidy, manufactured feed. I discovered that feeding rate did not influence catfish natural prey ingestion and natural prey preference in general. Even though the feed was ingested by fish and increased fish growth, all the fish still ingested the same types and amounts

of natural prey through time. I also found it surprising that the catfish ingested larger insects and chironomid larvae during early life and then switched to smaller size zooplankton later, because the opposite pattern has been observed for most other fishes. From an applied aquaculture perspective, natural prey may have an important role in the growth of juvenile channel catfish during early life. Future studies should further examine the interactive effects of resource subsidies, habitat quality, and consumer ontogeny on diet patterns in highly subsidized ecosystems.

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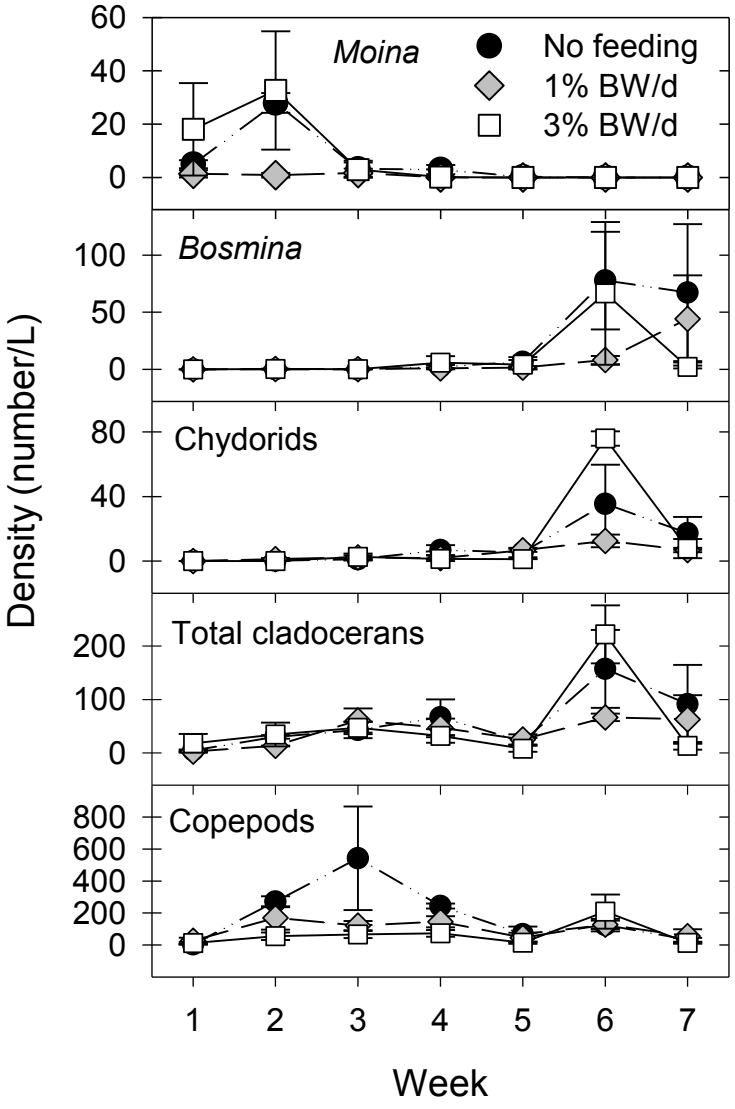

Figure 1. Comparison of zooplankton densities in ponds across feeding-rate treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010. Symbols represent mean ± 1 SE.

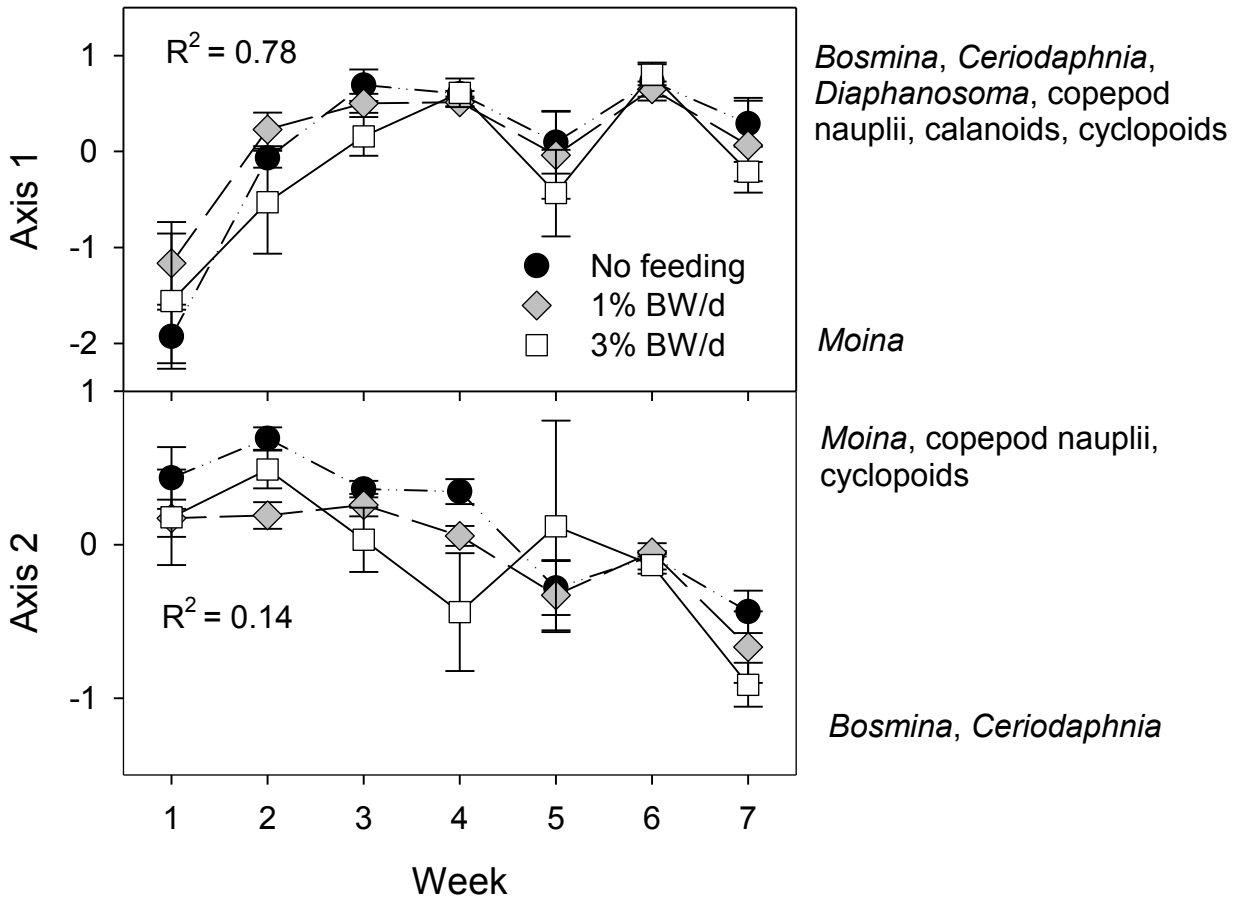

Figure 2. Temporal comparisons of natural prey assemblages in ponds that received no feed, 1%, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010. Composite axes of prey abundance in the ponds were derived from non-metric multidimensional scaling (NMS) of the seven most abundant prey taxa in the pond by biomass. R^2 values show the variance explained by each axis of the original dissimilarity matrix. Significant taxa correlations are listed to the right of each NMS axis in descending order of correlation strength. Symbols represent mean ± 1 SE.

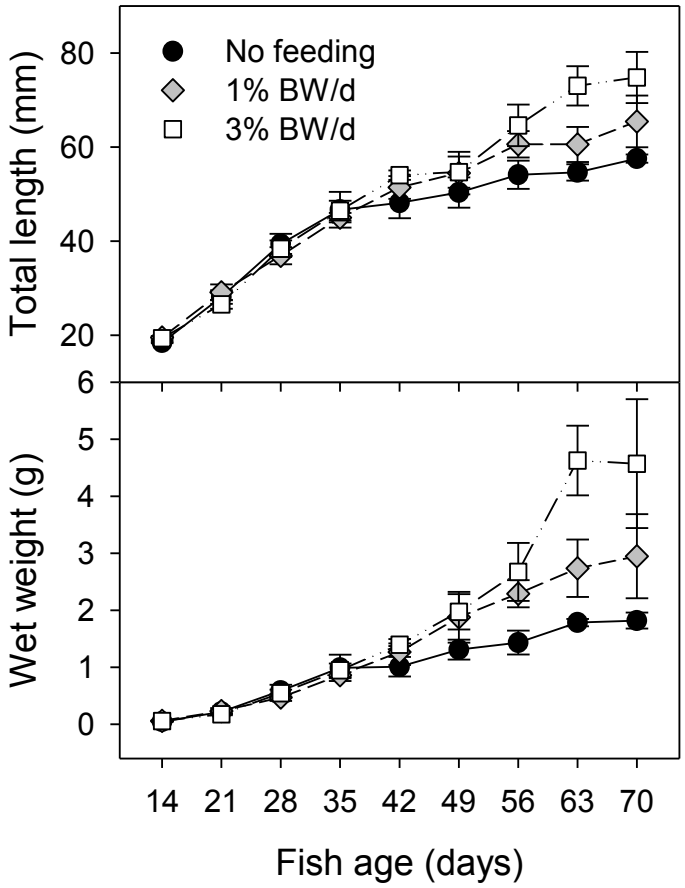

Figure 3. Comparisons of age-0 channel catfish growth in total length and wet weight across feeding-rate treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010. Symbols represent mean ± 1 SE.

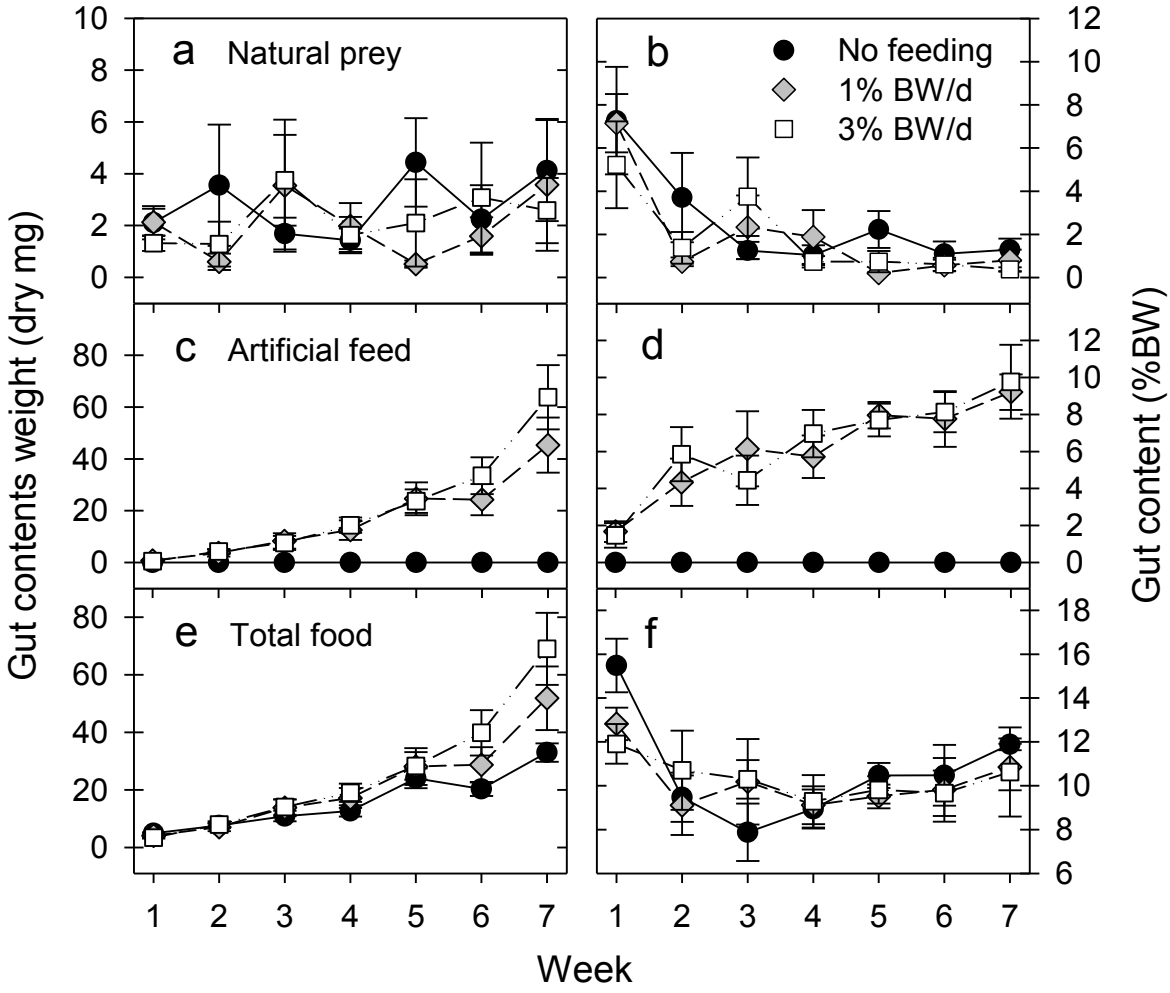

Figure 4. Comparisons of age-0 channel catfish (a,c,e) gut contents weight and (b,d,f) gut contents expressed as % body weight (BW) across feeding treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010. The contributions of (a,b) natural prey, (c,d) feed, and (e,f) all foods to the gut contents are shown. Symbols represent mean ± 1 SE.

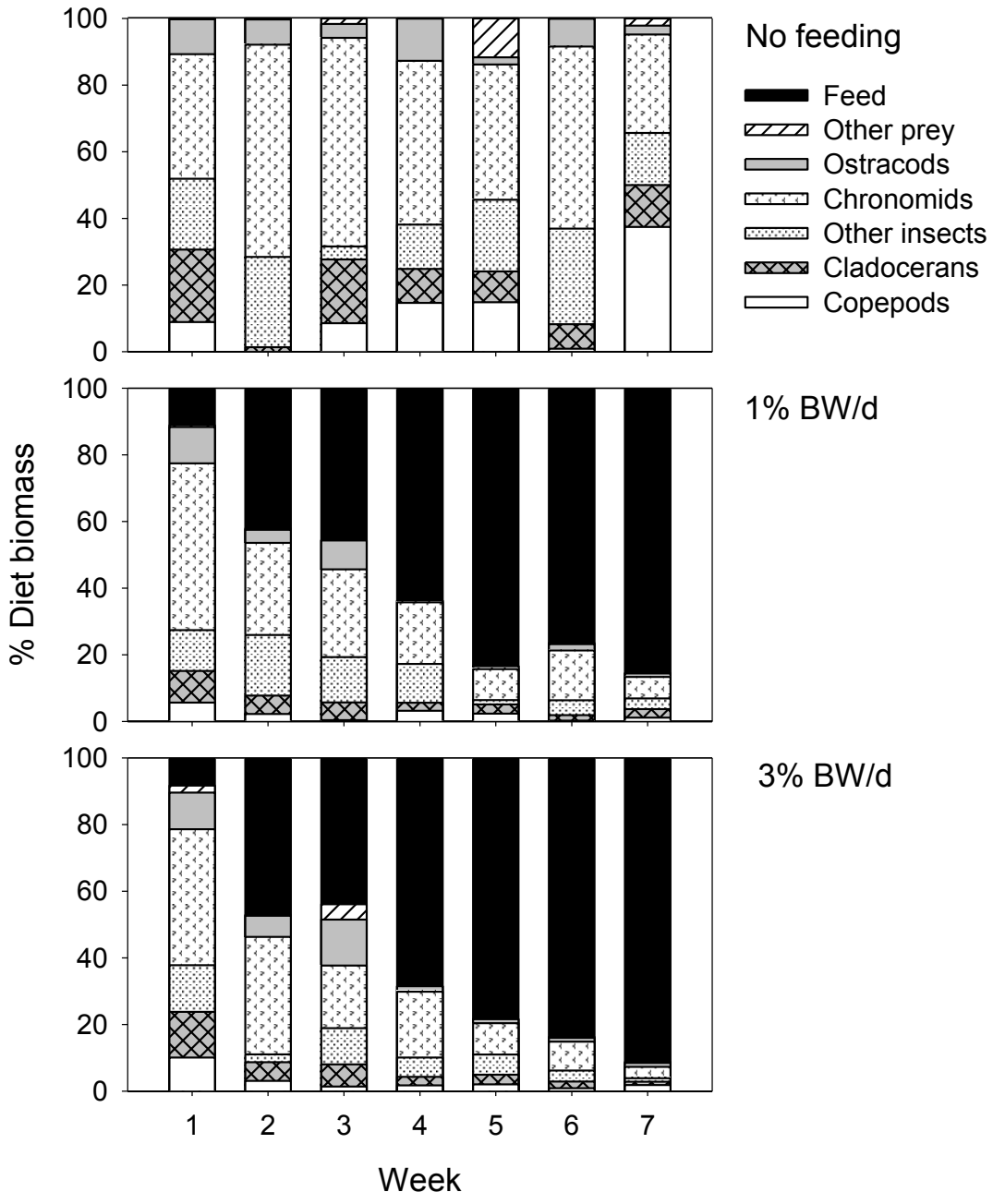

Figure 5. Comparisons of age-0 channel catfish diet compositions by biomass across feeding treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010.

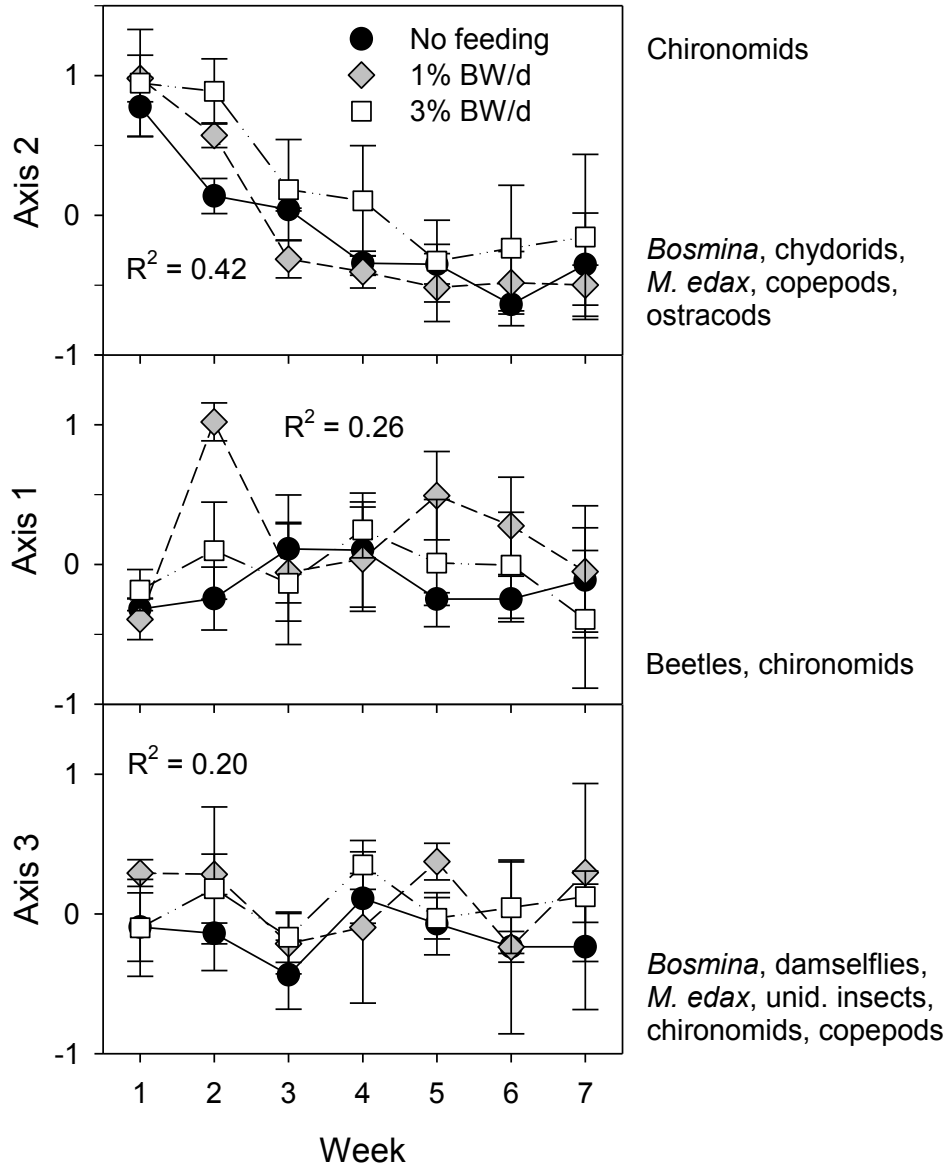

Figure 6. Temporal comparisons of natural prey assemblages ingested by age-0 channel catfish that received no feed, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010. Composite axes of covarying prey abundance in the gut contents were derived from non-metric multidimensional scaling (NMS) of the nine most abundant prey taxa in the guts by biomass. R^2 values show the variance explained by each axis of the original dissimilarity matrix. Significant taxa correlations are listed to the right of each axis in descending order of correlation strength. Symbols represent mean ± 1 SE.

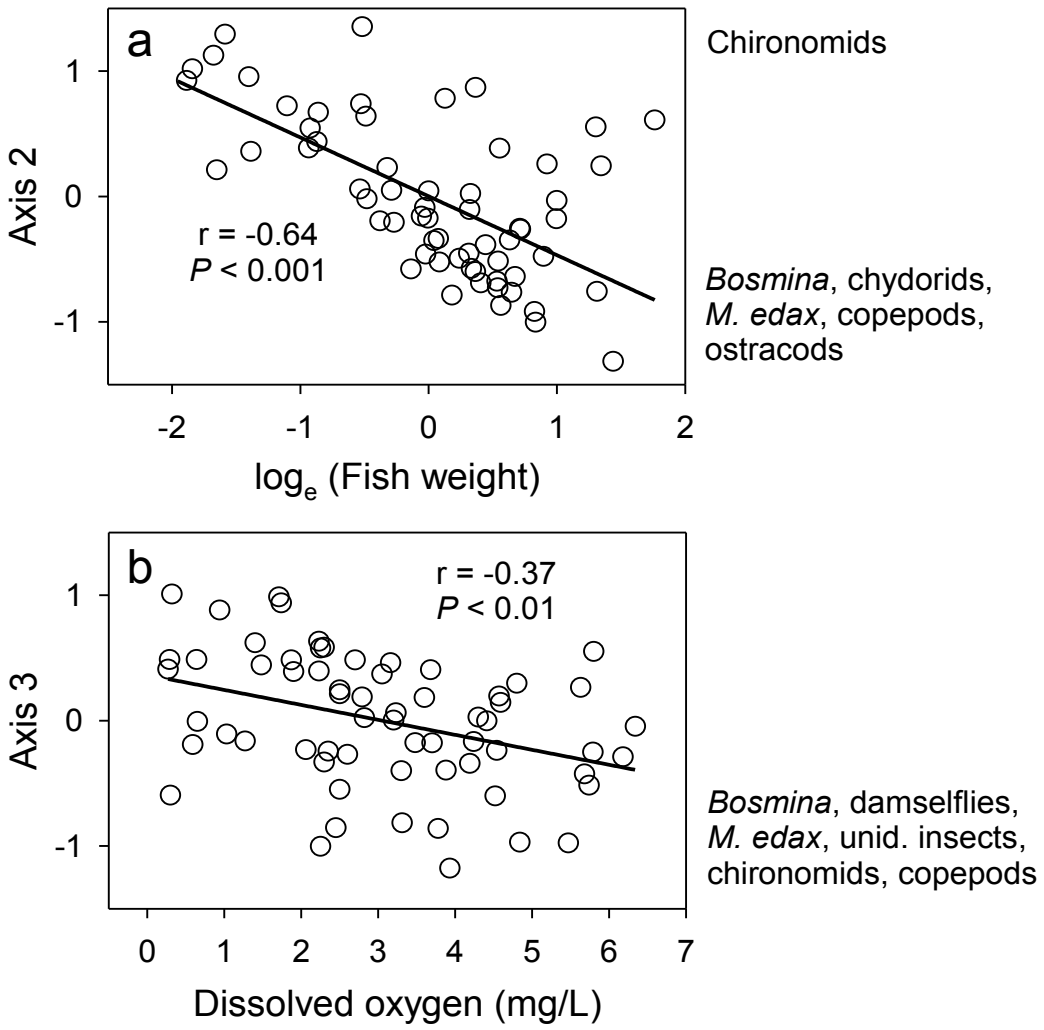

Figure 7. Significant correlations between axis scores from the NMS performed on age-0 channel diets and potential factors (temperature, dissolved oxygen concentration, and fish size) underlying fish diet composition at the Hebron State Fish Hatchery during July–August 2010. The listed taxa to the right of the panels are significantly correlated with the given NMS axis. The negative correlation between (a) Axis 2 and fish weight shows the increasing inportance of zooplankton in the fish diets as the fish grew in size, whereas the negative correlation between (b) Axis 3 and dissolved oxygen (DO) concentration shows that fish diets included more benthic zooplankton and insects in their diets when DO concentrations in the ponds were highest.

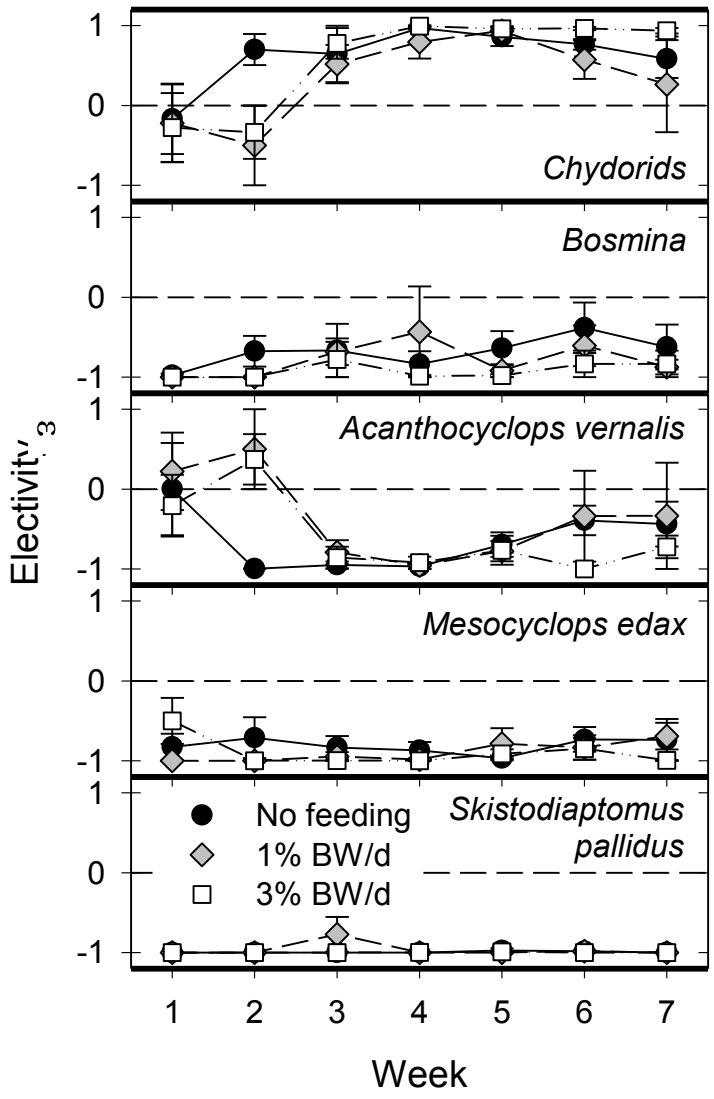

Figure 8. Comparisons of age-0 channel catfish taxonomic electivities (Chesson 1983) for natural prey across feeding treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at Hebron State Fish Hatchery during July–August 2010. Symbols represent mean ± 1 SE.

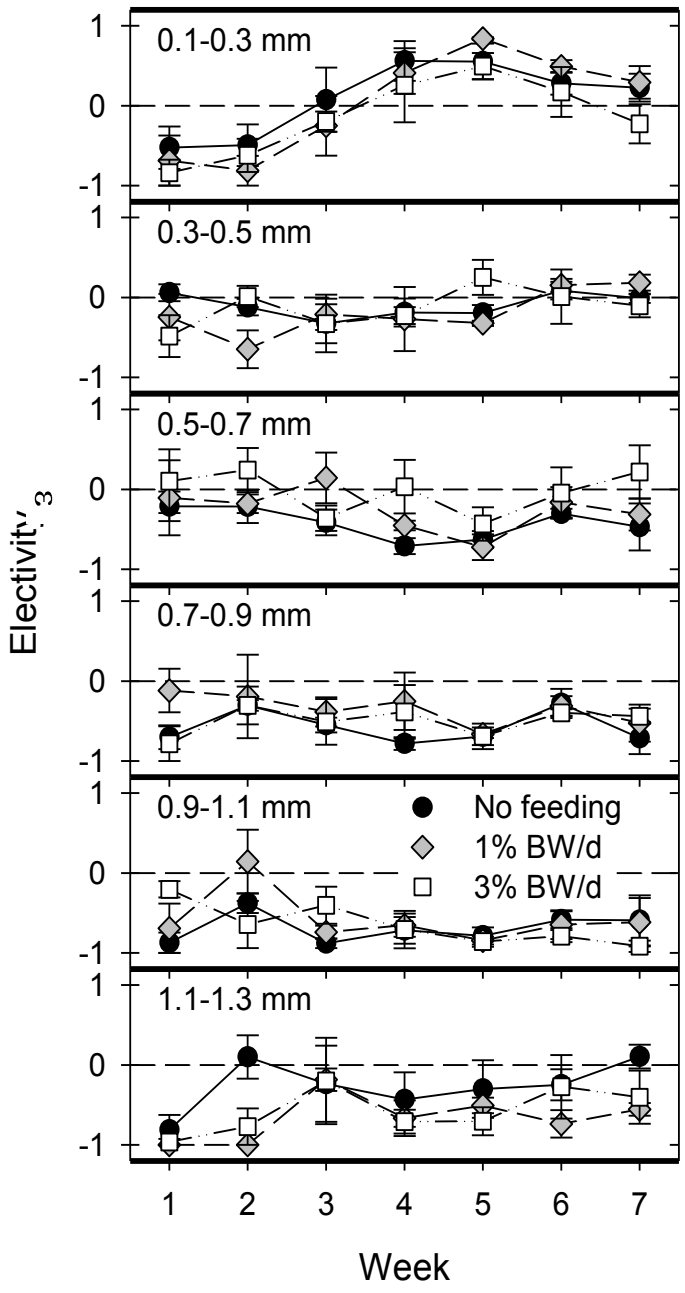

Figure 9. Comparisons of age-0 channel catfish size-based electivities (Chesson 1983) for natural prey across feeding rate treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at Hebron State Fish Hatchery during July–August 2010. Symbols represent mean ± 1 SE.

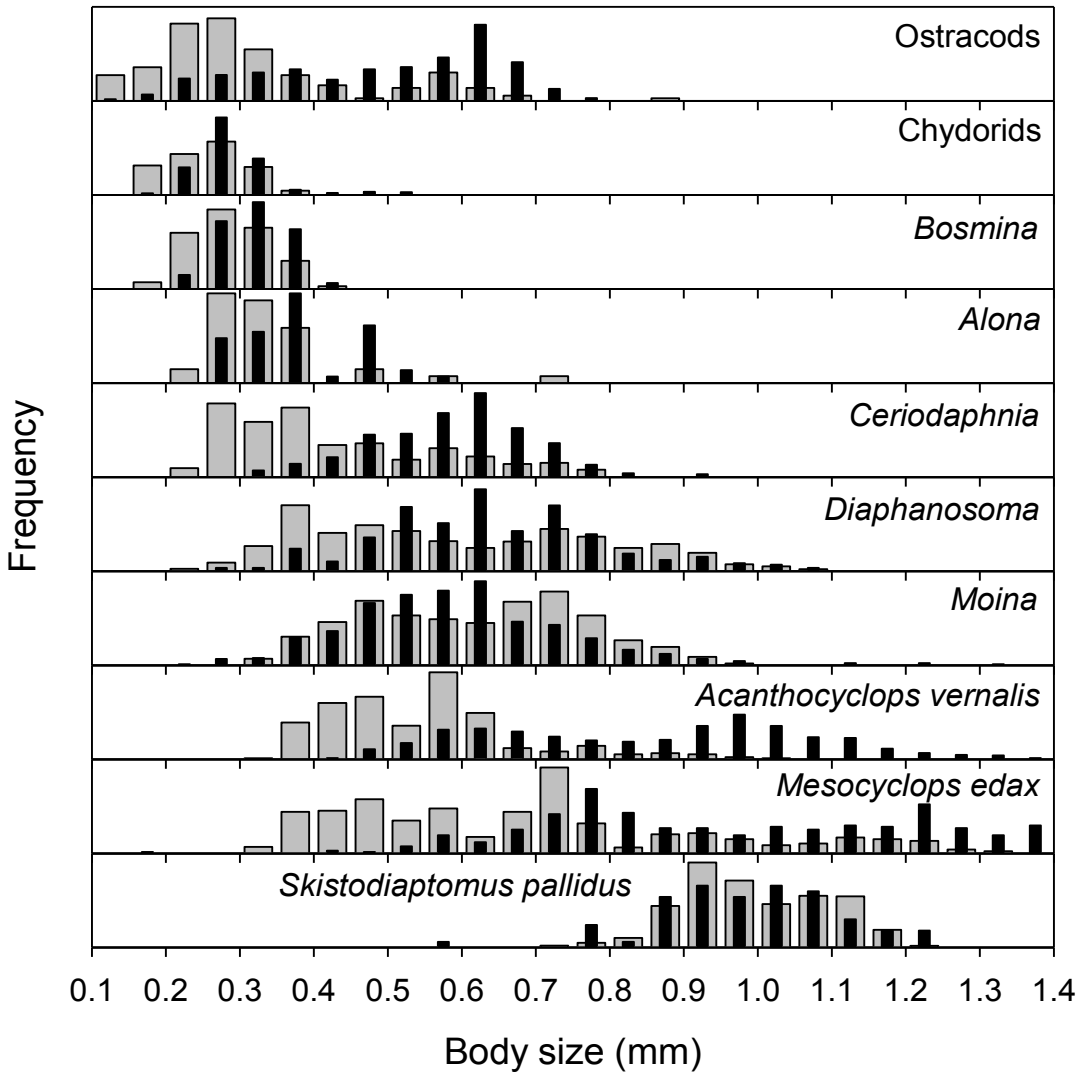

Figure 10. Comparisons of natural prey sizes collected in ponds (gray bars) and in the fish gut contents (black bars) for abundant taxa ingested by fish at the Hebron State Fish Hatchery during July–August 2010. Zooplankton size measurements in ponds and fish diets were pooled across all ponds and dates.

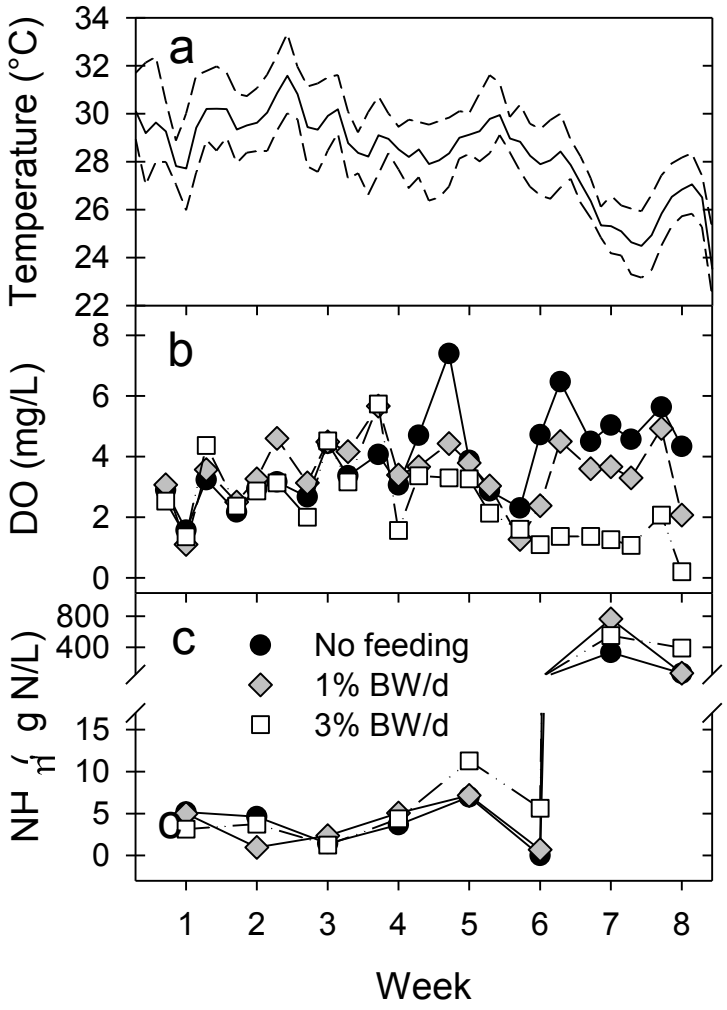

Figure 11. (a) Surface temperature variation and comparisons of (b) surface dissolved oxygen (DO) and (c) free ammonia (NH_3) concentrations across feeding-rate treatments of no feeding, 1%, or 3% body-weight/day (BW/d) at the Hebron State Fish Hatchery during July–August 2010. For panel (a), the solid line represents the mean daily temperature across all ponds, whereas the dashed lines represent the minimum and maximum observed temperatures. For panels (b,c), symbols represent mean values, and error bars are omitted to improve clarity.

Appendix A. Estimated fish biomass, diets and granular feed sizes, feeding schedules, and total feed applied during the 2010 pond experiment conducted at Hebron State Fish Hatchery. All diets had similar formulations with 52–54% crude protein and 12–16% fat, respectively, based on minimum manufacturer guarantees.

Dates	Fish biomass (kg/ha)[a]			Diet	Grain size (mm)	Feeding rations (kg ha^{-1} d^{-1})		Feed added (kg/pond)[b]	
	0%	1%	3%			1%	3%	1%	3%
12–25 July	5	6	5	A	< 1	0.15	0.47	0.6	1.9
26 July–6 Aug	57	44	52	A	< 1	0.32	0.94	1.3	3.8
7–13 Aug	95	83	92	B	1	1.1	4.4	2.3	9.1
14–19 Aug	97	122	134	C	2	2.2	6.7	3.6	10.9
20–27 Aug	126	181	190	C	2	3.5	8.9	8.2	21.8
30 Aug–7 Sept	138	221	257	D	3	5.7	14.6	16.3	42.2
7–13 Sept	175	286	440	D	3	6.7	16.8	10.9	27.2
14–30 Sept	231	294	309	E	4	3.5	8.9	17.7	47.2
						Total feed added (kg/pond)		61	164

[a] Based on average size of fish collected at the beginning of each period for each treatment, assuming 100% fish survival

[b] Feed mass added to each pond during the given period

Appendix B. Length-dry weight regression coefficients, dry weight, mg =a (length,mm)^b, with coefficients of determination (R^2), or mean dry weights (mg) used to calculate the biomass of natural foods ingested by age-0 catfish during 2010 at the Hebron State Fish Hatchery.

Taxon	Length- dry weight regressions			Mean weight	Source
	a	b	R^2		
Ostracoda	2.29×10^{-7}	2.978	0.96	-	Rodríguez-Pérez and Baltanás 2008
Chaoborus larvae	0.000677	1.48	0.89	-	Johnston and Cunjak 1999
Chironomid larvae (head cap width)	4.86	3.15	0.35	-	Johnston and Cunjak 1999
Chironomid larvae (body length)	0.00215	2.71	0.84		Johnston and Cunjak 2000
Chironomid pupae	-	-	-	0.2296	Meyer 1989
Dytiscid larvae	-	-	-	0.1029	Meyer 1989
Coleoptera adults	0.0077	2.91	-	-	Benke et al. 1999
Odonata nymphs	0.14	2.27	0.90	-	Sabo et al. 2002
Unidentified insect	0.1	2.37	0.91	-	Sabo et al. 2002
Hydrachnidia	-	-	-	0.1047	Meyer 1989
Nematoda	-	-	-	0.0174	Meyer 1989
Oligochaeta (Naididae)	-	-	-	0.0122	Meyer 1989